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Simulating Population Dynamics in an Ecosystem Context Using Coupled Eulerian-Lagrangian Hybrid Models (CEL HYBRID Models)

John M. Nestler and R. Andrew Goodwin

April 2000

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Simulating Population Dynamics in an Ecosystem Context Using Coupled Eulerian-Lagrangian Hybrid Models (CEL HYBRID Models)

by John M. Nestler, R. Andrew Goodwin

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Ecosystem Management and Restoration

Ecosystem Modeling



Simulating Population Dynamics in an Ecosystem Context Using Coupled Eulerian-Lagrangian Hybrid Models (CEL HYBRID Models) (ERDC/EL TR-00-4)

ISSUE: The Corps of Engineers is required to address ecosystem-level impacts of its projects, to develop plans that guarantee sustainable development, and to restore heavily impacted ecosystems. However, the tools to predict impacts and thereby develop project and restoration alternatives at an ecosystem level are either unavailable or have not received widespread acceptance.

RESEARCH OBJECTIVES: The objectives of this research report are to develop and describe a framework for incorporating population and community dynamics into ecosystem-level assessments. These tools can be applied singly or in concert with other tools and methods that describe the physical environment and hydrobiogeochemical processes having ecosystem significance.

SUMMARY: Higher trophic-level species (including many species that are threatened, endangered, commercially valuable, recreationally valuable, or important to ecosystem function) are difficult to simulate in an ecosystem context. CEL Hybrid models are a new method for coupling Eulerian and Lagrangian reference frames so that the higher trophic levels of an aquatic ecosystem can be systematically and realistically simulated. In this approach, standard

Eulerian models are used to simulate hydraulic and water quality within an ecosystem of interest. A spatially explicit population model is overlaid on the hydraulic and water quality model. The Eulerian-Lagrangian couple works as follows: the influence of aquatic organisms on water quality is evaluated by spatially averaging relevant characteristics of the organisms within a cell (an Eulerian concept), such as biomass, while the population dynamics of individual species (e.g., reproduction, recruitment, feeding, migration, and/or mortality) are modeled in a spatially explicit manner by treating organisms as individuals or groups of individuals (a Lagrangian concept). CEL Hybrid models can alternate between the Eulerian and Lagrangian reference frames so that higher trophic levels can be simulated with minimal distortion and loss by exploiting the advantages and minimizing the disadvantages associated with each separate framework.

AVAILABILITY OF REPORT: The report is available on Interlibrary Loan Service from the U.S. Army Engineer Research and Development Center Library, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199; telephone (601) 634-2355.

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Preface

The U.S. Army Corps of Engineers is required to address ecosystem-level impacts and to develop plans that guarantee sustainable development. This report identifies and describes selected approaches for incorporating population and community dynamics into ecosystem-level assessments. These tools can be applied singly or in concert with other tools and methods that describe the physical environment and hydro-biogeochemical processes having ecosystem significance.

This report was prepared by the U.S. Army Engineer Research and Development Center (ERDC), Environmental Laboratory (EL), Waterways Experiment Station (WES), Vicksburg, MS. This study forms part of the Ecosystem Management and Restoration Research Program (EMRRP) Work Unit 33067, "Modeling Techniques for Predicting Ecosystem Impacts and Managing Resources." The EMRRP is sponsored by Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to WES under the management of EL. Dr. Russell Theriot, EL, is the Program Manager for the EMRRP. The HQUSACE Technical Monitors for EMRRP are Ms. Denise White, Mr. Pete Juhle, Ms. Cheryl Smith, and Mr. Ted Rugiel.

This report was written by Dr. John M. Nestler, Water Quality and Contaminant Modeling Branch (WQCMB), and Mr. R. Andrew Goodwin, contract student, WQCMB, under the general supervision of Dr. Mark S. Dortch, Chief, WQCMB, EL; Dr. Richard E. Price, Chief, Ecosystem Processes and Effects Division (EPED), EL; and Dr. John Keeley, Acting Director, EL. Complete in-house technical reviews were performed by Ms. L. Toni Schneider, Mr. Tom Cole, and Dr. Patrick Deliman, WQCMB, and Dr. Robert Kennedy, Ecosystem Processes and Effects Branch, EPED.

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1 Introduction

Background

Scientists and policy-makers have become increasingly aware that many of the values and services provided by healthy ecosystems cannot be adequately assessed by examining limited attributes of the physico-chemical environment or by restricting evaluations of impact to a limited number of living resource categories. Ecosystems cannot be assessed by examining only limited subsystems, because ecosystems have emergent properties that can only be described when the system in its entirety is considered. That is, the interplay between variables that result in observed ecosystem structure and function cannot be described when only a limited subset of an ecosystem is analyzed. Federal Agencies have committed to an ecosystem perspective in their actions (Beattie 1996; Dombeck 1996; and Goodman 1996), although with some constraints (Morrisey 1996). Presently, tools necessary for U.S. Army Corps of Engineers (CE) scientists and engineers and others in the Federal sector to systematically predict or assess ecosystem impacts at multiple hierarchical levels are either unavailable or have not received the peer acceptance necessary for widespread use (Reichman and Pulliam 1996). Without tools to manage impacts at an ecosystem level, the many benefits of healthy ecosystems to society such as seafood, forage, timber, recreational benefits, and aesthetic values cannot be achieved (Daily 1997).

CE construction activities, regulatory functions, and operation and maintenance of water resources projects can have profound effects on the physical environment as well as on the living resources that depend on the physical environment. In addition, the Corps may partner with or support agencies whose activities, separate from the Corps, can have substantial impacts on the environment. The Corps presently monitors, predicts, evaluates, minimizes, and mitigates impacts of its activities on selected aspects of the physico-chemical environment and on individual species or guilds of populations but generally does not consider entire ecosystems or watersheds in its assessments, although there are noticeable exceptions. Typically, the Corps focuses on a limited spatial scale and a limited number of living resources categories. For example, in a reservoir setting a typical analysis may address whether or not inpool and downstream water quality standards are being met and

may consider effects on a limited number of sport fishes. However, a systematic analysis of ecosystem-level effects is not currently employed by the Corps.

The present state of the art can be separated into two distinct mathematical traditions to study and evaluate natural systems (King 1993). Population modelers have used certain difference equations, sometimes called the Lotka-Volterra system of equations, to describe population dynamics and to explore the influences of competitors, predators, and resource availability on populations. However, the leap from simple population models to investigations of communities and ecosystems in natural settings was generally too profound to be addressed by the population modeling paradigm. However, the population modeling tradition sensitized ecologists to the value of using mathematical descriptions of complicated biological processes as a way of exploring and understanding natural systems. The population modeling tradition is still used extensively and, as in the past, continues to make contributions to our understanding of population-level processes. The most recent advance in population modeling, made possible by improvements in computational power, is the individual-based population model (Deangelis and Gross 1990). In this approach, individuals of a species are simulated, although each virtual individual may represent from one to many individuals (e.g., LePage and Cury 1997). Various other population aggregation strategies may be employed as well; for example, eggs and larvae may be simulated in an eulerian framework, and juveniles and adults may be simulated by an individual-based model (Rose et al. 1996).

To date, the most comprehensive models attempt to simulate the underlying physics and chemistry of aquatic systems. These mass-balance (they simulate the movement of mass of constituents as well as energy) models are often two- or three-dimensional (2-D, 3-D) and are commonly used by CE environmental engineers and scientists to predict and assess water quality changes associated with water resources activities. These models discretize the aquatic environment into a series of cells, within which water quality (WQ) processes are dispersed. Complex flow fields in the aquatic environment, which are often modified by water resources activities, are simplified as patterns of streamlines and flow vectors/velocities. Chemical and hydraulic inputs are processed and routed using established equations to predict water quality patterns (Thomann and Mueller 1987). This simulation approach works well for physical and chemical processes that can be spatially averaged into cells (Figure 1, left plot) and, if sufficient numbers of compartments are used, can provide both an understanding and predictive capability for lower trophic levels (e.g., Gin, Guo, and Cheng 1998).

From the perspective of 2- and 3-D water quality models, an ecosystem is viewed mathematically as families of equations representing a large number of connected compartments. These equations attempt to describe the basic underlying physical and chemical processes of ecosystems. Typically, energy and mass within a compartment are transformed and then exchanged with other compartments and various sinks and sources (e.g., Cassell et al. 1998). Ecosystem ecologists assess impact in terms of trends, stability, persistence,

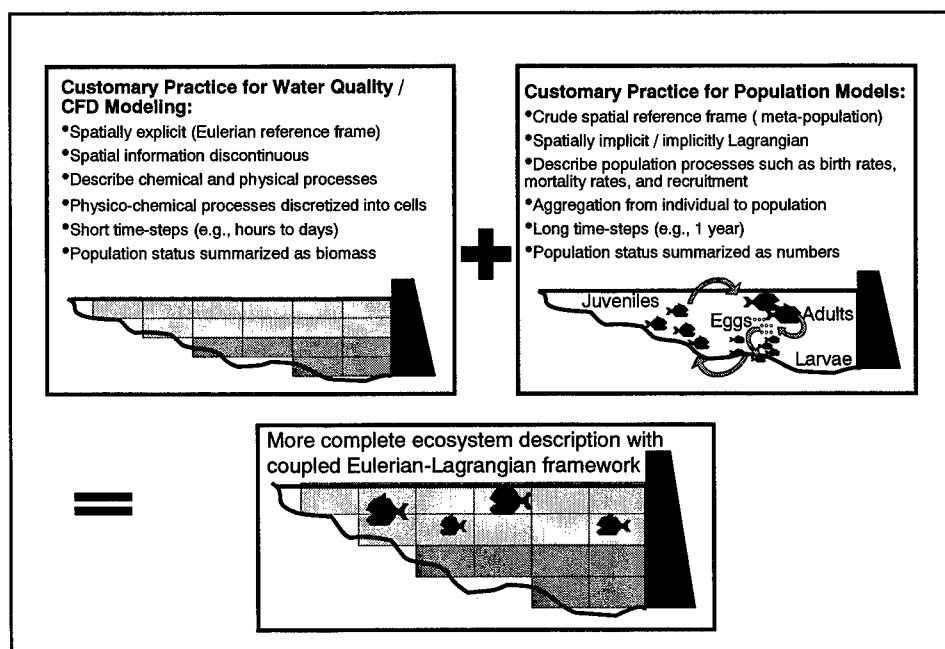


Figure 1. Differences between water quality/hydraulic models common in engineering and population models common in biology. A more complete ecosystem prediction capability is possible if the two modeling traditions could be combined into a single, systematic framework

response relative to goals or standards, and other metrics that characterize and summarize the behavior of the system. This approach, while powerful, is usually characterized by large supporting data collection studies that require extensive modeling and mathematical expertise and long durations for completion. However, once complete, the model becomes a surrogate for the real system. Once calibrated, the system can be perturbed by changing boundary conditions or inputs to represent changes imposed by various management alternatives. Scientists and engineers can evaluate various project alternatives using the model much more efficiently, quickly, and cheaply than attempting to evaluate alternatives by trying out each alternative on the real system. This approach can be used to avoid alternatives that have undesirable outcomes. Summary results from the modeling effort can be passed onto decision-makers. However, using this simulation approach limits the ability of the engineering sector to realistically simulate higher trophic levels such as fish, shellfish, and other large, or abundant, mobile organisms (Marcus and Boero 1998) which may exhibit complex suites of behavior that have ecosystem-level importance (e.g., Breitburg et al. 1997), but are difficult to describe using mass-balance approaches (Murtaugh and Kollath 1997).

Because of their complex behavior and daily-to-seasonal movements, individuals from large or abundant mobile species are difficult to average and disperse into the cell structure normally used in hydraulic and water quality models to discretize the aquatic environment (e.g., Breitburg et al. 1997). Figure 2 graphically displays how population dynamics are normally forced into

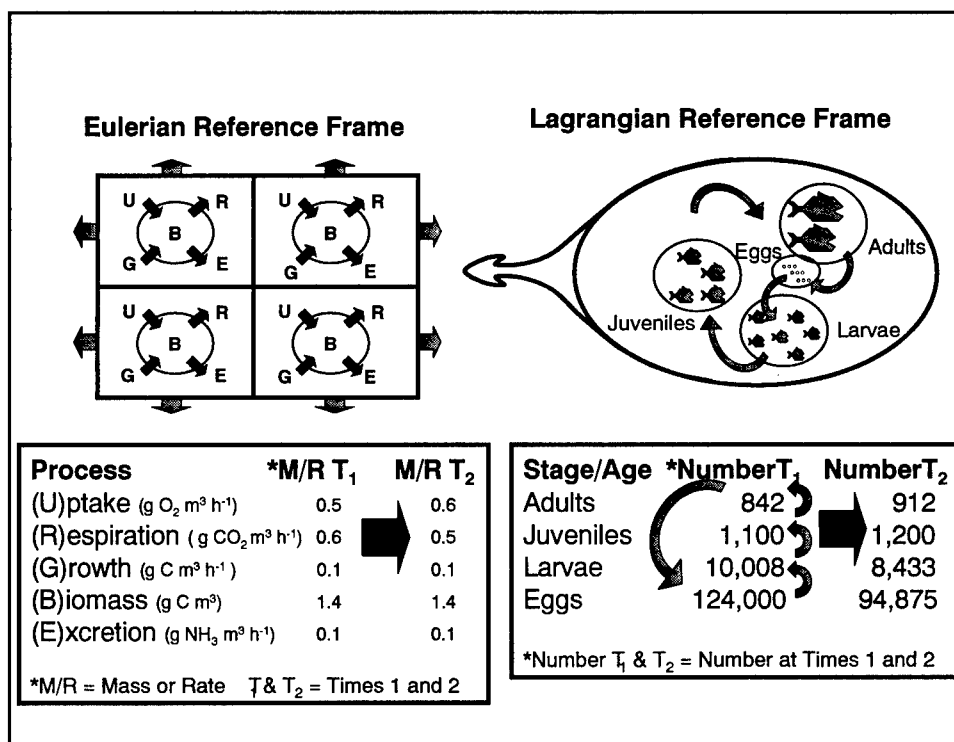


Figure 2. Graphic representation of the differences between typical water quality models (Eulerian reference frame) and population models (implicit Lagrangian reference frame). Note that the Eulerian reference frame spatially discretizes an ecosystem into cells with each cell containing cell-averaged (uniform) constituent concentrations. Any information about the spatial distribution of biota at scales less than the scale of discretization is lost

the Eulerian framework, typical of most hydraulic and water quality models. Note that population numbers must be converted into mass and then averaged by cell. Therefore, all population processes must either be described in terms of the mass of standing crops within each cell (e.g., a population is represented as grams of carbon per unit volume as opposed to a tally of individuals) or as exchanges of material (fluxes) between cells (e.g., growth is represented as increased accumulations of carbon as opposed to an increase in the number of individuals). Capturing the population dynamics of a highly mobile species in such a reference frame is difficult, because their population dynamics or their interaction with the rest of the ecosystem may be based on complex movement behavior of individuals or groups of individuals. Individuals that contribute to interpopulation, intrapopulation, and ecosystem processes are neither evenly distributed in time or space and, therefore, cannot be easily averaged for placement into an Eulerian reference framework. In addition, the structuring factors in food web organization may not be clear (Murtaugh and Kollath 1997), thereby making it difficult to assign species in a food web into trophic levels. Averaging errors also occur when members of many different species, each with specific relationships with the rest of the ecosystem, are lumped into relatively few trophic levels, obfuscating the response of individual species or life-stages

to changing environmental conditions. As a consequence of transforming population numbers into biomasses and lumping many life-stages and species into a few trophic levels, ecosystem models can be applied only with difficulty to address issues associated with management of individual species, biodiversity, population risk assessment, and restoration of threatened or endangered species.

In contrast to the multidimensional water quality models often used by the engineering sector, population models typically focus on keystone species or on a particularly valuable or endangered species, which is often used as a surrogate for ecosystem health. Population models usually have long time-steps reflecting the reproductive cycle of the target species (typically, 1 year), and the simulated environment is minimally discretized. These models usually predict the number of individuals of a population in each life-stage or by age but do not directly predict biomass. Furthermore, most population models are spatially implicit (i.e., spatial and/or process information unique to the ecosystem under study does not enter into the population model – e.g., Figure 3, right plot). While the type of ecosystem being simulated is taken into account, characteristics unique to the ecosystem are often not incorporated in a way that allows its unique dynamics to influence populations (Figure 2, top left plot). For instance, a modeler may use the latitude of a lake to adjust for the number of eggs produced per female or use the number of degree-days to determine the time it takes juvenile fish to develop into adult fish. Detailed information based on unique spatial attributes or processes of the system being analyzed usually does not enter into population models. In short, the temporal and spatial resolutions of most population models are generally incompatible with the temporal and spatial resolutions needed for hydraulic and water quality predictions.

Ecosystem structure and function can be separated into subsystems that operate at different temporal and spatial scales (Webster 1979; Ahl and Allen 1996). The relationships between the ecosystem and population modeling paradigms become apparent when they are related to a hierarchical view of ecosystem structure. One of many different possible hierarchical organizations is presented in Table 1. Mass-balance models are typically used to simulate and explore those ecosystem processes that are easily discretized into cells. That is, mass-balance models are useful for simulating processes that occur at temporal and spatial scales favorable to cell-averaging. Processes that are difficult to average into cells are not well simulated using mass-balance models. The population dynamics of highly mobile, large, or abundant biota such as fish that may be responsible for structuring parts of aquatic ecosystems (Quirós 1998; Gonzalez and Tessier 1997; Dettmers and Stein 1992; Devries and Stein 1992) are particularly difficult to capture using mass-balance approaches and are usually best described using one of many different formulations of population models (e.g., Gurney et al. 1998, Winkle et al. 1998) (Figure 3).

CE scientists and engineers have used both modeling traditions to predict, avoid, minimize, and mitigate the effects of water resource activities. However, assessments of water resources activities are typically constrained to a limited spatial scale, analysis of a limited number of water quality processes, and/or analysis of the dynamics of only a limited number of living resources. For

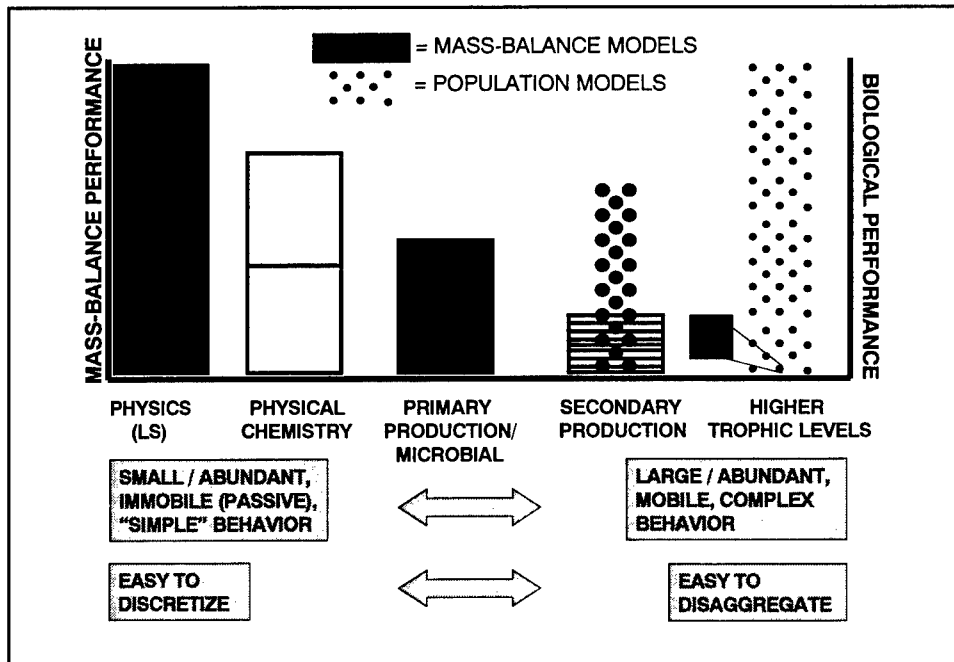


Figure 3. Relative performance of typical modeling approaches for processes or components of ecosystems of different temporal or spatial scales. Note that mass-balance models are typically used to simulate physico-chemical conditions and lower trophic levels. Population models, with the most extreme example being individual-based models, are typically used when individual species are the focal point of the simulation

Table 1 Typical Example of Hierarchical Organization of Ecosystems (many variations on this theme are possible)		
Category (Level)	Examples	Tools to Simulate/Assess
Large-scale physics	Bulk-flow of water	Computational fluid dynamics
Physico-chemical dynamics	Chemical oxygen demand	Simple water quality models
Primary production / respiration	Photosynthesis/respiration	Complex water quality models
Secondary production	Lower trophic levels (Zooplankton)	Mixed
Higher trophic levels	Fish and wildlife	Population model (Sometimes linked to other models)

example, a typical analysis for a reservoir setting may address whether or not in-pool and downstream water quality standards are being met and may consider effects on a limited number of sport fishes. For many ecosystems, this is a serious shortcoming. In some cases, the chemico-physical environment cannot be adequately predicted and assessed without considering feedbacks from higher

trophic levels (Schaus et al. 1997). Similarly, higher trophic levels cannot be adequately predicted and assessed without considering feedbacks from chemico-physical processes of the ecosystem (Michaletz 1998). For example, Persson et al. (1996) describe a lake setting in which a complex interplay among two piscivorous fish species, the zooplankton community, and stratification patterns determines the dynamics and distribution of fish and zooplankton.

Full ecosystem-level analyses are rarely performed. A typical assessment for a terrestrial setting may use population risk assessment based on relatively simple population models, but the population models are seldom coupled to models that can accurately predict the physico-chemical environment. In contrast, multidimensional water quality models are routinely coupled to multidimensional hydraulic models to predict long-term water quality patterns in reservoirs, rivers, and estuaries as part of operational optimization, environmental impact studies, compliance, or restoration actions. However, multidimensional water quality models seldom realistically simulate the population dynamics of higher trophic levels such as fish and wildlife.

Problem

Without tools to assess the ecosystem-level impacts of water resources activities, sustaining the benefits derived from ecosystem-level processes such as seafood, forage, timber, recreational benefits, and aesthetic values is difficult. Ecosystems have emergent properties that can only be assessed when the system is considered in its entirety. Currently, there is a chaotic collection of differing models, strategies, and approaches for simulating ecosystems, and there are no methods to routinely and systematically couple water quality and population models. Ideally, the solution for achieving ecosystem-level assessment is to create a new modeling paradigm by combining hydraulic/water quality models and population models. However, hydraulic/water quality models and population models are very different (Figures 3 and 1) with each having considerable and very different strengths and weaknesses. Consequently, multidimensional hydraulic/water quality models are not directly coupled with population models in the present state of the art with the goal of improving the performance of both water quality and population predictions, although water quality and hydrodynamic models have provided input to population models (Rose 1998).

Many new issues facing the Corps cannot be addressed using only one or the other of the two modeling traditions. Presently, there are few tools available that allow systematic and simultaneous prediction and assessment of both water quality dynamics and the population dynamics of higher trophic levels such as abundant fishes, sport fishes, or endangered fish and wildlife species. As a consequence, restoration planning for threatened and endangered species is uncertain, impact assessment on valuable natural resources is problematic, ability to fully manage risk associated with contaminants and toxic materials is hindered, and natural resource management for biodiversity is limited.

Objective

The objective of the research documented in this technical report is to show how two different mathematical approaches that appear to be divergent actually supplement one another. These two frameworks can be coupled together into a new framework that can be systematically and realistically used by Corps scientists and engineers to better assess and manage ecosystem-level impacts. We describe how the population dynamics of higher trophic level populations can be coupled with the physico-chemical processes of the aquatic environment. This method uses a new technique that allows realistic simulation of multiscale ecosystem processes by maximizing the benefits associated with two different modeling frameworks. The method couples the Eulerian reference frame typical in hydraulic/water quality models with the implied Lagrangian reference frame typical in population models. This report describes the conceptual basis for coupled Eulerian-Lagrangian (CEL) HYBRID models. This report builds on a workshop held during July 1997 in Winrock, AR (Waide and Gandy 1998), and a case-history application of a CEL HYBRID model will be published next year.

2 Logical Foundation and Description of CEL HYBRID Models

Alternative Reference Frameworks Used in Modeling

The key to developing a new modeling approach is to identify unifying concepts between the contrasting engineering and biological modeling traditions for simulating aquatic ecosystems. The Lagrangian framework maintains the integrity of an object as it moves through simulated space (Figure 4, upper plot). On the other hand, the Eulerian framework does not maintain the integrity of a transported object as it moves through simulated space. In the Eulerian framework, items located in the system are treated as if they are well dispersed and spatially averaged within a cell (Figure 4, lower plot).

Each modeling framework has its strengths and weaknesses for simulating portions of ecosystems. From a water quality perspective (or Eulerian perspective since most, but not all, water quality models are Eulerian), population models can be viewed as being implicitly positioned within one large cell (i.e., the environment in which the population lives is considered to be uniform). For example, the lake depicted in Figure 5 (top left plot) can be thought of as comprising one cell in which all of the water quality processes have been averaged (i.e., there exists only one uniform environment). An individual in a population, a group of individuals, or the entire population can be symbolically represented as a particle (i.e., a point in space) contained in the one-cell Eulerian system representation. We develop a comprehensive, logical framework to convert the implicit spatial depiction of population models into an explicit depiction that conceptually allows population models to be coupled with Eulerian water quality models.

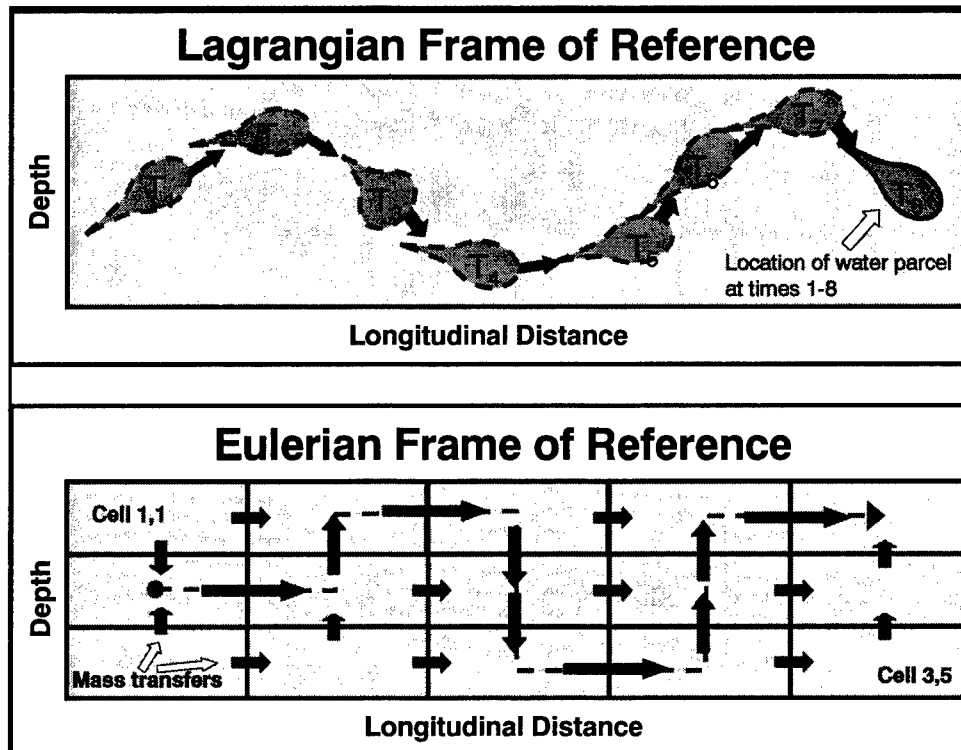


Figure 4. Schematic of the Lagrangian frame of reference (upper plot) and the Eulerian frame of reference (lower plot)

Coupling Eulerian and Lagrangian Frameworks with Particle Tracking Logic

The use of a particle tracking algorithm to couple the Eulerian and Lagrangian frameworks is an important, but only the first step toward developing an ecosystem simulation tool. Since Eulerian-based hydraulic/water quality models only provide discontinuous spatial information (Figure 4), the ability to track the continuous path of a particle (a surrogate for a fish or other mobile aquatic organisms) through a flow field is not inherent in typical hydraulic/water quality models.

A solution to this problem is the use of a particle tracking algorithm (Chapman, Gerald, and Dortch 1994, Martin and McCutcheon 1999). Particle tracking is a commonly employed technique for simulating the path of an idealized neutrally buoyant, passive particle through a simulated hydraulic field. A particle tracking algorithm works by: (a) obtaining hydraulic information at nodes or faces of an Eulerian cell, (b) interpolating the hydraulic information to obtain necessary values at various interior points within the cell, and (c) using the information at these interior points to move the particle in the cell (Figure 6). A particle tracking algorithm provides the means necessary to couple Lagrangian (biological population) and Eulerian reference frames (Figure 7) for a more

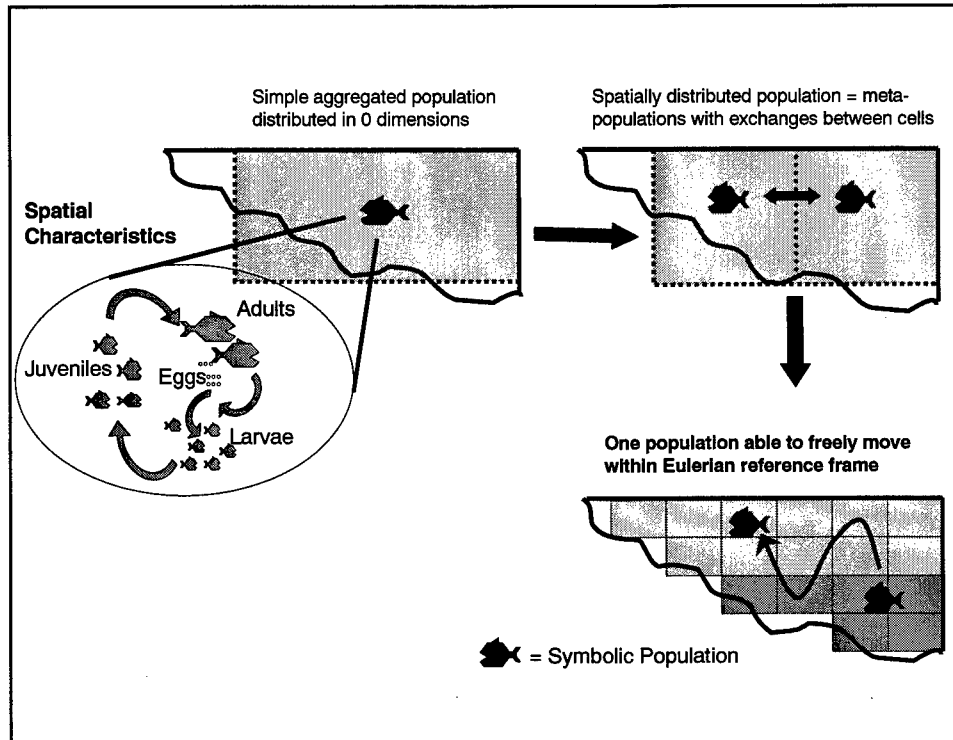


Figure 5. Reconciling the spatial differences between population models and water quality models

complete ecosystem-level analysis than either approach can provide by itself. It takes discontinuous information and allows one to interpolate to intermediate points of interest to generate a nearly continuous information field instead of having information limited to arbitrary points in the grid corresponding to the cell structure of the Eulerian reference frame (Martin and McCutcheon 1999).

The particle tracking algorithm can be modified to provide a framework for simulating the swim path selection of fish or other aquatic organisms using the following steps. Velocity vectors u (X-direction), v (Y-direction), and w (Z-direction) are obtained from the hydraulic model at nodes or faces (Figure 7, top panel). This information is used to calculate a predicted position of a fish for the next time-step assuming passive transport. If hydraulic and water quality conditions between the present and anticipated position are evaluated by appropriate "stimuli-response rules," the particle can be influenced to move in a manner different than simple passive transport (Figure 7, third panel). "Stimuli-response rules" based on observed fish behavior transform the passive particle into a virtual fish, thereby, creating a Numerical Fish Surrogate (NFS) which can emulate the movement of real fish (i.e., virtual fish "swim" to new positions obeying a behavioral rule). In Figure 7, a virtual fish moves as a passive particle in the X- and Y-direction but moves in the direction opposite to passive transport in the Z-direction. If the hydraulic cues, or "stimuli-response rules," aquatic organisms use to navigate through the hydraulic environment can be estimated, then it is possible to program these rules into a particle tracking algorithm (Rose

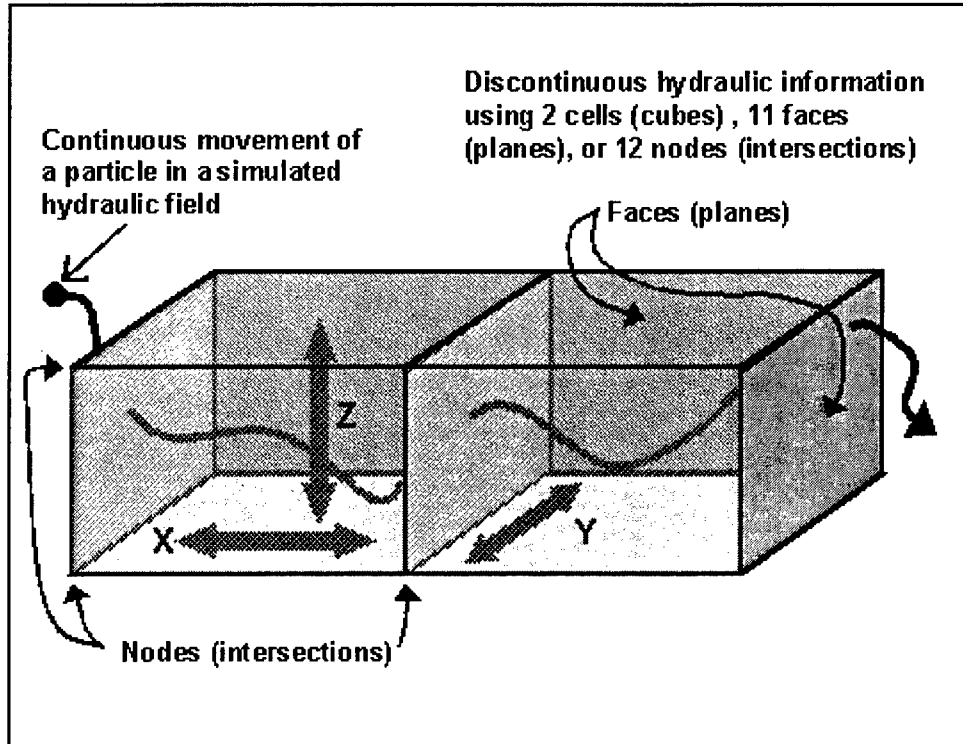


Figure 6. Reconciling trajectory information (Lagrangian frame of reference) and hydraulic/water quality information (Eulerian frame of reference)

1998). However, it is important to verify the accuracy of the particle tracking algorithm for passive particles. This can be done using a variety of methods including verifying the model to data obtained from drogues released into the system being studied.

Water quality variables can also be incorporated into stimuli-response rules. For example, virtual fish could avoid low dissolved oxygen (DO) or high-temperature areas if programmed with appropriate rules. If the particle tracking algorithm is properly programmed, calibrated, and verified (or if field measurements of the hydraulic grid are accurate and of sufficient resolution), it is then feasible to use virtual fish to move through a virtual ecosystem and assess the movement response of natural fish populations to various water resources activities. If virtual fish movement is, in turn, coupled to a population model or water quality model, then the coupled models can be used to assess the effects of ecosystem-level changes on a single species and to feed back the responses of the species to the water quality model.

Continuous-Time Markov-Chain Behavioral Models

The key element in developing a strategy to couple the two frameworks is to develop a framework for simulating the movement of large or abundant animals

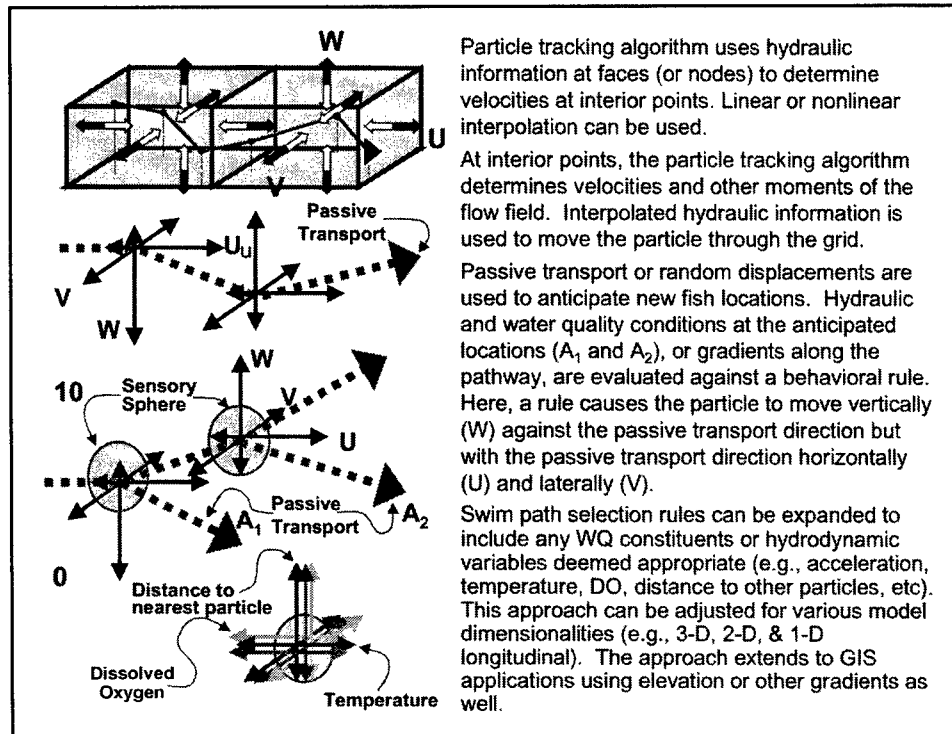


Figure 7. Velocity vectors at faces, or at any other points, in the two-cell system are used to determine the velocity vectors at points of interest in the interior of the cells (upper panel). These interpolated velocity vectors can be used to determine the movement of a neutrally buoyant object entrained in the flow field at incremental time-steps (passive transport – second panel). Using this approach, a particle can be moved continuously through virtual space even though the hydraulic model, or field measurements, only provides information at points or faces. The third panel describes the transformation of passive transport into swim path selection of fish. Fish can be considered to exist as a particle in virtual space. Using their sensory systems, they are able to acquire hydraulic information in their immediate vicinity represented here by a 3-D eclipse. They use the information they acquire to make decisions about the swim path they will follow. The use of hydraulic information can be expanded to include water quality or biotic information that can be provided by the model (fourth panel)

within an ecosystem. Animal behaviorists often use continuous-time Markov-Chains (CTMC) for describing complex behavior of individual animals (Figure 8) (Haccou and Meelis 1992). Use of statistical models based on CTMC provide the most comprehensive concept for simulating animal movement behavior and, therefore, provide the optimum strategy for coupling the two modeling frameworks commonly employed within the Corps of Engineers.

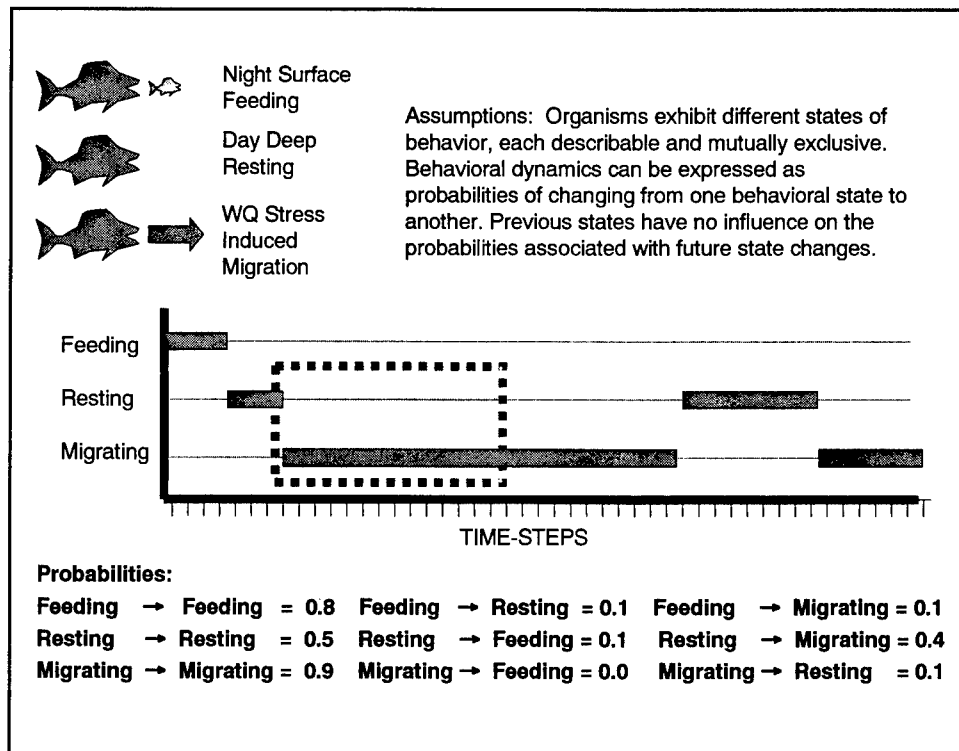


Figure 8. Schematic showing how CTMC can be used to develop the fish swim path selection rules necessary to simulate complex fish behavior given hydraulic or water quality data. A Markov-Chain can represent a system with multiple, mutually exclusive states with specific probabilities for changing from one state to another

A Markov-Chain can represent a dynamic system consisting of several distinct, mutually exclusive states with specific probabilities for changing between states. In a behavioral system, a Markov-Chain representation requires that an individual organism exist in one of a number of distinct, describable, and mutually exclusive behavioral states. For example, a fish can exist in three separate behavioral states: resting, feeding, and migrating with unique probabilities for changing between each state. The probability of moving from a “feeding state” to a “resting state” may be 0.1 at each time-step. For a given species and state of behavior, rules can be established to predict the behavior of individual organisms. For example, in the migration state, a reasonable rule for adult salmon behavior in a 3-D hydraulic field may be to maximally swim in the X-direction against passive transport (i.e., to swim upstream against the current as fast as possible), to select the Y – location that minimizes the downstream water velocity (i.e., find the lateral position in the channel that has the lowest U-velocity (in the X-direction) so the fish spends the least amount of energy needed to move upstream), and to swim at a depth having the least turbulent flow.

The CTMC statistical model facilitates the reproduction of complex behavior using states of behavior and responses of organisms to hydraulic, acoustic, or

water quality information based on the current behavioral state. Different stimuli-response rules can be employed within each distinct behavioral state since it is unlikely a fish, for example, would move similarly in the daytime as it would at night, nor would it move the same during spawning and nonspawning times. Most long-term applications of CTMC require substantial numbers of states, since the response of organisms to the flow field may depend on water quality, time of day, season of the year, lifestage, time since last feeding, and/or other factors, all of which must be represented as "states of behavior." State-specific random movement is captured by a random displacement term scaled to the swimming capabilities of the target taxon that can be included for any spatial dimension being simulated. Optimum behavioral rules using CTMC are obtained by minimizing the error between predicted and observed swim path selections using statistical methods often associated with calibration and verification.

Depicting individuals of a population as particles recognizes the duality that large, mobile organisms may exhibit. That is, they have some attributes which are best simulated using a Lagrangian reference frame and other attributes which are best simulated using an Eulerian reference frame (Figure 9). The first, step is to separate the attributes of populations into those that are best simulated in a Lagrangian reference frame and those that are best simulated in an Eulerian reference frame. For example, the Lagrangian reference frame is ideal for simulating processes such as mortality, recruitment into the adult population, and fecundity (reproductive potential). The Eulerian reference frame is best suited for simulating chemico-physical processes such as respiration and nutrient regeneration.

Depicting an organism, or group of organisms, as a single particle that moves within a cell is the conceptual building block for complex simulations of ecosystem-level processes. Development of the conceptual framework can be thought of as follows: A semipermeable barrier is placed in a lake so that the lake becomes two, nearly separate, water bodies (Figure 5, top right plot). From the population modeling perspective, there are now two populations (typically, this is referred to as meta-populations; models used to simulate meta-populations are referred to as meta-population models), each one represented as a number of particles. Migration between the two populations (i.e., through the semi-permeable barrier) is permitted. From the Eulerian perspective, the lake is now represented as two cells. Each cell has unique hydraulic and water quality attributes. Different water quality and/or hydraulic conditions in each cell may lead to different behavior in each cell for the same type of organism or group of organisms.

It is possible to use water quality constituents, such as temperature, to segregate the water body into different zones (e.g., thermal stratification, Figure 5 bottom right plot). If the location of a population (i.e., individuals, sub-populations, or the entire population) is tracked, then it is possible to update behavioral characteristics of the population based on water quality or other conditions unique to its cell location.

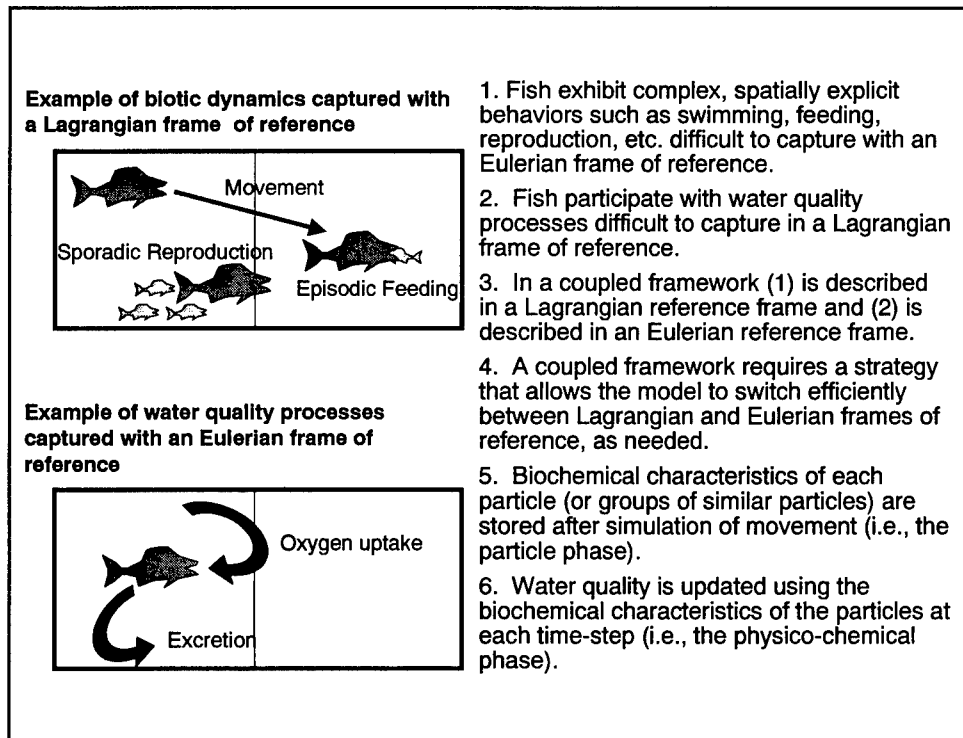


Figure 9. Combining the Eulerian and Lagrangian reference frames into a single, useable modeling framework

The procedure for coupling the two independent reference frames (Eulerian and Lagrangian) for use in ecosystem modeling is shown in Figure 10. In the first time step, the particle tracking algorithm portion of the NFS is used to distribute the simulated fish among the grid cells. After distribution, each portion of the population participates in selected biological processes such as death, birth, or recruitment into the next age/size stage. These biological processes are influenced by local water quality and hydraulic conditions. After the simulated fish have participated in selected biological processes, they are categorized based on an appropriate criterion into stages (e.g., eggs, larvae, juveniles, and adults) or ages (e.g., 0-year olds, 1-year olds, 2-year olds, and 2+ year olds). Biomass, or other Eulerian-based variables, can then be determined using conversion factors to convert numbers of organisms into appropriate chemical constituents. Once the required Eulerian-based variables are determined, the simulated fish can then influence water quality (e.g., through nutrient release, growth, and oxygen uptake).

Using particles to represent fish provides an added flexibility. Fish can be aggregated differently to fit the analysis. For example, in Figure 11 (left plot) one particle represents an entire population. Another alternative is to allow each particle to represent an individual organism (Figure 11, right plot). In population modeling, such a representation is termed an individually based population model (IBM). Obviously, there is a gradient from which to choose the appropriate particle representation. Each particle could represent from one to many individuals of equal size, age, sex, or stage depending upon the complexity

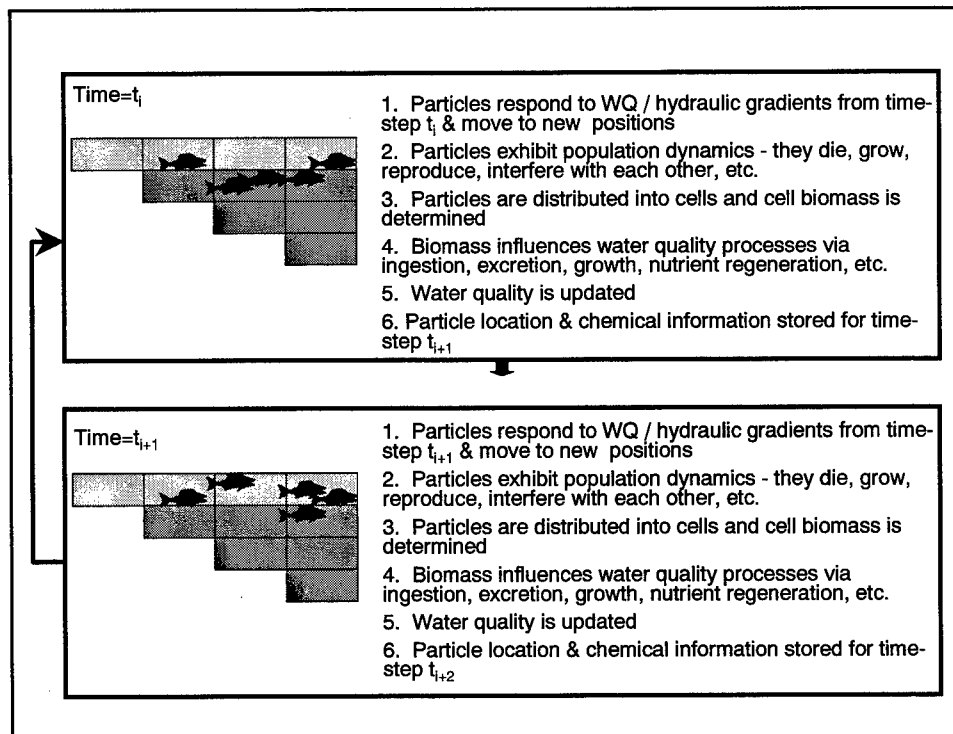


Figure 10. Procedure for Coupling Eulerian and Lagrangian reference frames

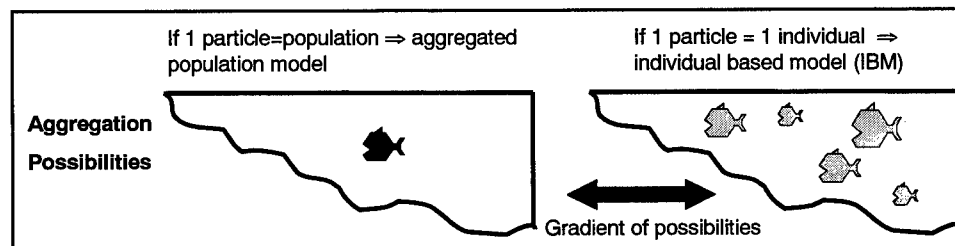


Figure 11. Extremes of population aggregation: one particle = one population or one particle = one individual

of the problem, the speed of the computer, or other factors that might influence the level of aggregation necessary to address a particular issue.

3 Capabilities and Limitations of CEL HYBRID Models

Improved Capabilities

CEL HYBRID models have improved capabilities over population models and water quality models that result from their use of a unified Eulerian and Lagrangian reference frame.

Mathematical Accuracy

To represent natural systems, mass-balance models must average mobile biota into cells and convert density of organisms from numbers per unit volume or area into biomass per unit volume or area. Consequently, dynamics that occur based on the behavior of individual organisms cannot be simulated with these models because individuals have been averaged out. The dynamics of populations optimally simulated by individual population models cannot be emulated by mass balance models or simulated indirectly by adjusting biomass with coefficients (or functions), such as coefficients that account for density dependence. While food web models have some advantages over trophic models, trophic models also commonly average life-stage and population dynamics into boxes.

Predictions made by mass-balance models may differ from predictions made by models that consider individual elements of a system, or small aggregations of elements (particularly individual population models), in those situations when the interactions between individuals of a population may influence the results of a simulation. For example, consider a hypothetical ecosystem comprised of 30 cells (Figure 12). The interactions between individuals of differing cells can be ignored if densities do not exhibit substantial temporal or spatial variability because the interactions can be treated as a constant (Figure 12, upper plot) within the analysis. However, if densities do exhibit substantial temporal or

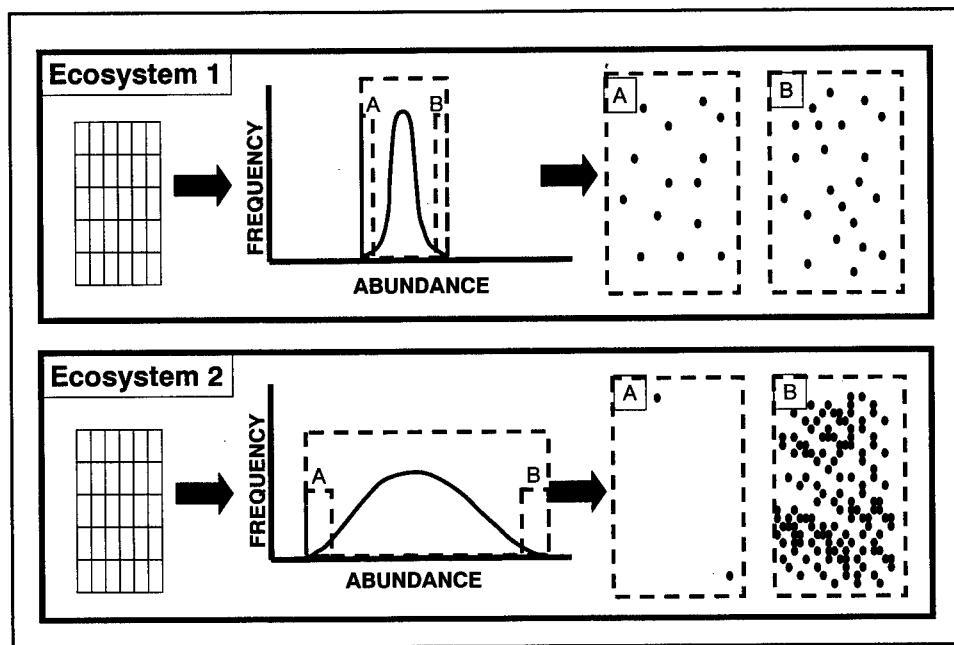


Figure 12. Comparison of two ecosystems having different ranges of values for a variable best described as a particle. In Ecosystem 1, the mean concentration is not high and the difference in density between the two tails of the distribution is not great. As a consequence, the effect of the interaction between particles can either be ignored in the analysis or treated as a constant. In Ecosystem 2, the difference in density between the two tails of the distribution is great and changes in interactions between particles can affect the simulation

spatial variability, then the type or degree of interactions between individuals may also change substantially (Figure 12, lower plot) - a situation not easily handled by mass-balance models but easily addressed by population models. In a lake setting, for example, a mass-balance model may predict a transformation of minnow biomass into bass biomass even under very low minnow density. However, a model that considers interactions among individuals may show no transformation of minnow biomass into bass biomass because under low densities, a bass may never encounter a minnow.

Ecosystem-Level Risk Assessment Using CEL HYBRID Models

Population models are used as the basis of risk assessment for issues commonly involving individual species and the effects of contaminants and toxic materials (or other stressors) on population numbers. Population models vary in complexity, but typically a modeler must estimate fecundity, density dependence, and survival, either for ages or stages of the population. The modeler cannot provide a single estimate for any of the population vital statistics

but instead will select their estimates from a distribution because of multiple sources of uncertainty (Figure 13). Population dynamics are simulated by randomly selecting the necessary coefficients from the distribution of coefficients. Typically, a baseline condition is simulated multiple times to serve as the basis of comparison (Figure 13, black arrows). Each run of the population model is different because the parameters to simulate the population are changing with each time-step of the model run. The model runs are summarized as the probability, or risk, that at a reference time the population abundance will decrease to certain threshold values.

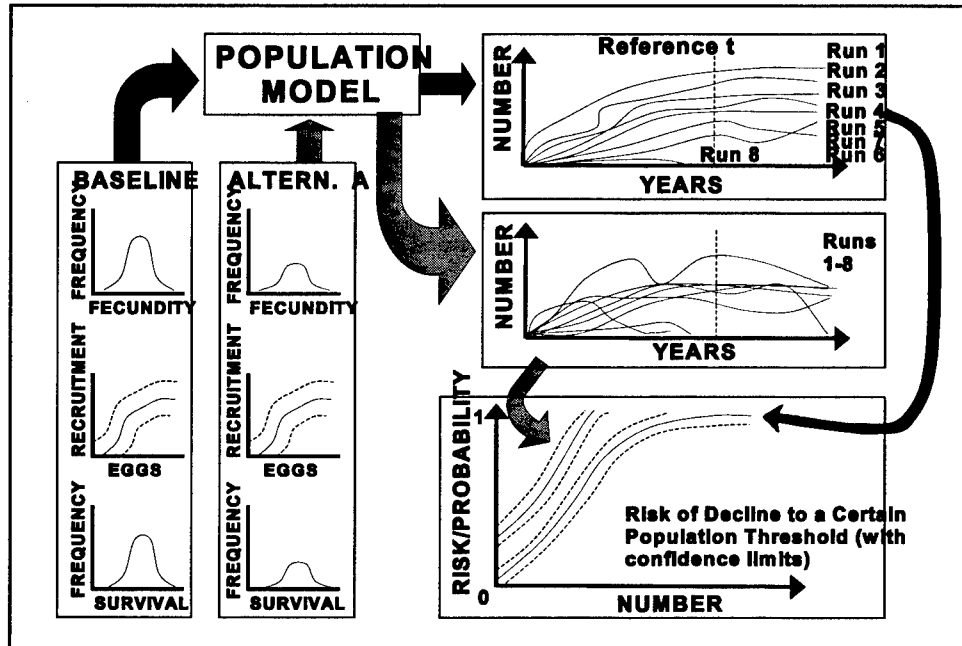


Figure 13. Flow diagram of typical population-level risk assessment. Distributions of coefficients are established for the baseline (black arrow) and stressor (ALTERN. A - gray arrow) conditions. Both sets of coefficients are used by the population model to generate two families of model runs, one using coefficients typical of baseline conditions (black arrow) and one using coefficients associated with the stressor (gray arrow). Each family of model runs is summarized as the probability that the population will fall below certain threshold values at a predetermined reference time

The effects of a stressor are predicted using the same steps except that the coefficients used to estimate population dynamics are adjusted downward to represent the effects of a stressor. For example, fecundity or survival may be reduced in the presence of the stressor (Figure 13, gray arrows). Reduced fecundity or survival may result in depressed population numbers compared to the baseline conditions. Multiple model runs, with coefficients selected from the revised distributions, are then used to develop a family of model runs that includes the effects of the stressor. The model runs that include the effects of the stressor can then be summarized and compared to the baseline runs in terms

of the changes in risk associated with the stressor compared to the baseline. Multiple stressors or concentrations of stressors can then be assessed.

CEL HYBRID models allow for the partitioning of uncertainty in the relationship between coefficients and environmental variables. Consequently, the uncertainty in estimates of population coefficients can be partitioned into the uncertainty associated with each of the environmental variables, not just those associated with the stressor. Partitioning uncertainty into different components allows risk to be partitioned and managed at an ecosystem level. For example, a lake may have sediments contaminated with mercury. This same lake may contain a population of striped bass - a fish whose distribution within a lake is determined by water temperature and DO stratification. In a standard population model-based risk assessment, the effects of the contaminated sediments would be considered only in baseline (no contamination) and contaminated conditions. However, a CEL HYBRID model will allow operations to be included in the risk assessment by linking the movement of striped bass to stratification patterns within the reservoir. The CEL HYBRID model can be used to estimate dose-exposure for the fish (how much time each fish spends in areas of different stressor concentration) and thereby refine the effects of the stressor. Alternatively, the CEL HYBRID model can be used to evaluate the effects of different operations on water quality patterns and thereby affect the dose-exposure histories of striped bass (Figure 14). A CEL HYBRID model could be used to determine if raising the pool elevation by 2 ft minimizes the dose and exposure of striped bass in the reservoir. CEL HYBRID models can be used to consider and manage stressors in an ecosystem context and trade off the effects of natural stressors, such as elevated temperatures or low DO concentration, against the effects of contaminants or toxic materials (Figure 14).

Virtual Sampling

CEL HYBRID models combine the ability of mass-balance water quality models to simulate the physico-chemical environment with the ability of IBMs to realistically simulate the movement of mobile aquatic organisms in 3-D space - that is, CEL HYBRID models create a virtual ecosystem that can be sampled using virtual sampling gear. Unlike mass-balance water quality models (or mass-balance ecosystem models) in which organisms sampled with various gear types as individuals must be transformed into biomass, CEL HYBRID models can simulate organisms directly and individually, and the virtual reality of the model can be sampled with virtual sampling gear to allow direct comparison with real-world sampling gears without transformations (Figure 15). Virtual sampling can be burdened with all of the assumptions and inadequacies of real-world sampling to generate samples that have similar statistical characteristics (mean and variance) as real-world samples. Therefore, the step of transforming the abundance of a target species population from numbers per life-stage per meter to a variable such as grams per cubic metre is avoided along with the associated loss of information. The trade-offs between sampling gears can even be evaluated in CEL HYBRID models.

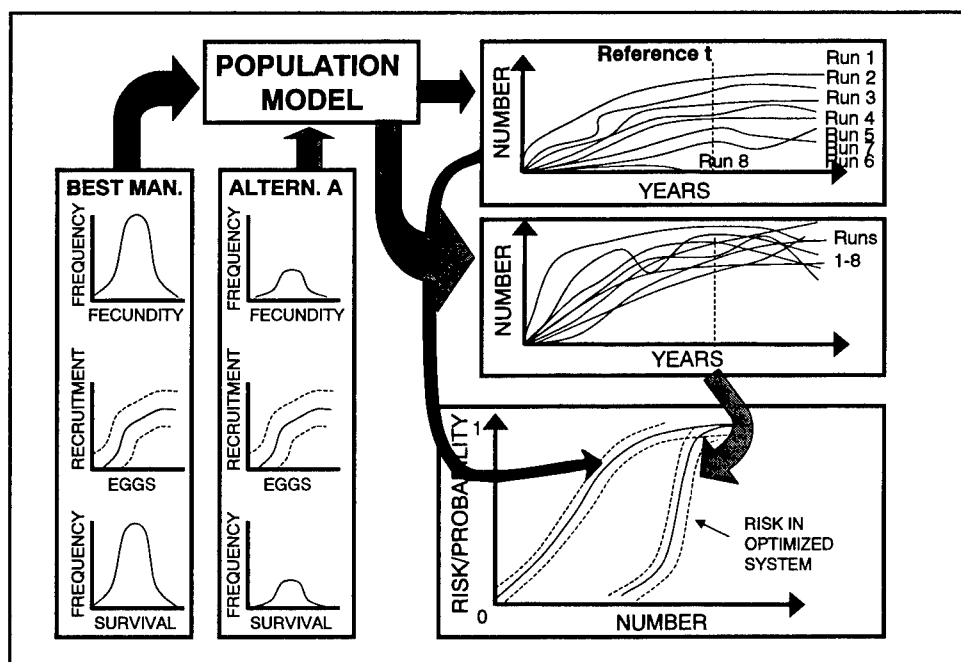


Figure 14. Flow diagram describing how CEL HYBRID models can be used to minimize the effects of natural stressors and toxic or contaminant materials using operations

Limitations of CEL HYBRID Models

As in any attempt to simulate reality, CEL HYBRID models are based on certain assumptions, require that the user employ diligence in applying this type of model, and may require extensive computational resources.

- a. The model must simulate the real world at a scale and resolution suitable to the target population. A CEL HYBRID model cannot provide a reasonable description of a population if relevant features in the real world are not adequately described in the model.
- b. The temporal scale of the water quality model must be small enough to simulate the movement of the target population. The time scale of the NFS must be of an interval sufficiently small to provide for realistic depictions of movement. However, the temporal scale of the water quality model and the temporal scale of the NFS can be different.
- c. The interpolation scheme used to estimate values of variables at various interior points of interest within a model grid cell must be reconciled with the sensory biology of the target taxon. Linear interpolation may be adequate for some conditions, but nonlinear interpolations may be required for those applications in which the target taxon's sensory system is sensitive to the higher derivatives of position. For example, without

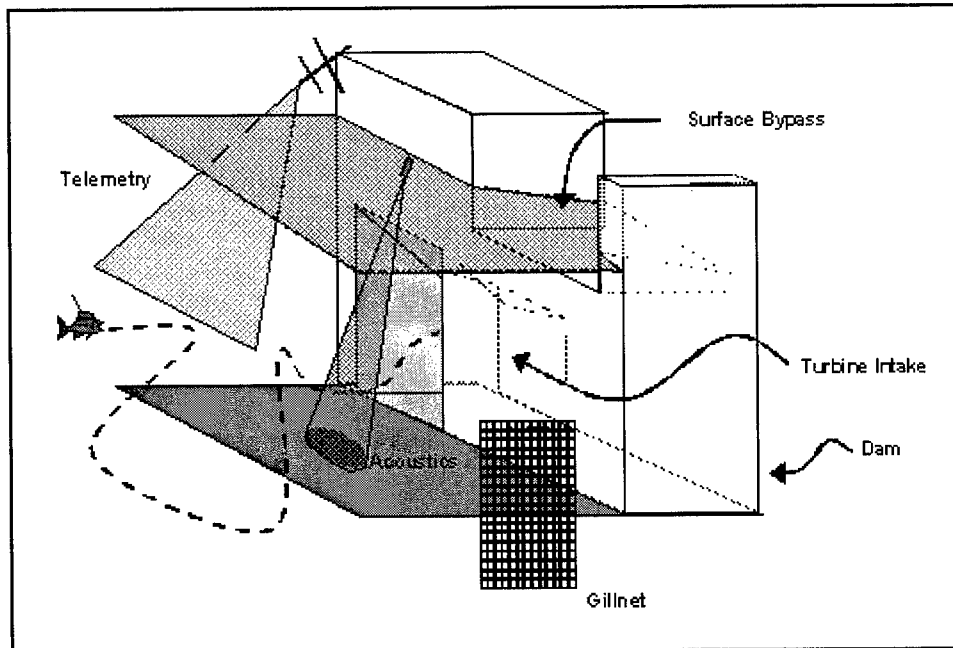


Figure 15. Virtual sampling using CEL HYBRID models is possible because the movement of fish is simulated. A gillnet can be represented as a plane with certain probabilities of capture or selectivity if encountered by a simulated fish. Similar approaches can be used to perform virtual sampling using hydroacoustics or biotelemetry. Virtual sampling allows direct comparison between the modeled system and the real system without transformation of information

visual cues, fish have no way of directly sensing velocity. However, fish are known to have sensory capability to detect minute changes in acceleration. Therefore, a nonlinear interpolation using information from the nodes of the cell in which a fish is located as well as information from neighboring nodes may be necessary to predict the movement of fish in a flow field.

- d. The modeler must correctly identify the variables that determine the movement of members of the target population. In some cases, variables responsible for movement may not be of equal importance and may require differential weighting.
- e. The modeler must also identify and simulate the appropriate number of behavioral states for the target population.
- f. The real world contains transients and random variables that are impossible to simulate. These effects may limit the usefulness of the model.
- g. Calibration and verification of movement, population, and water quality modules must be performed.

4 Summary and Conclusions

Theoretical Considerations

As pointed out by King (1993), there is no single correct model for any given application. This condition arises because ecological modeling generally is not based on first principles in the same way that physicists have studied and modeled the natural world. As a group, ecologists and biologists have been accused of having “physics envy,” because their concepts generally are not founded on first principles.

The best model for an ecosystem is itself (Figure 16, right pathway). Therefore, optimal ecosystem simulation would occur if an existing ecosystem could be duplicated, molecule by molecule, and its processes duplicated, nanosecond by nanosecond. Ideally, the duplicate ecosystem should also be replicated to increase the statistical rigor of the results. Various effects or alternatives could then be tested on the surrogate ecosystems. The effects of project alternatives could then be unequivocally investigated, described, and summarized and wise decision-making assured. Unfortunately, such detailed replication of natural ecosystems is not possible. In lieu of complete duplication, ecosystem modelers attempt to capture the most important aspects of ecosystem structure and processes in numerical models, fully realizing that the model is nothing more than a highly simplified version of reality.

In general, modelers have one of two major conceptual pathways that they follow to attempt to mathematically recreate natural ecosystems. A modeler may take an Eulerian perspective and discretize space into boxes or cells or a modeler may take a Lagrangian perspective and disaggregate reality into its finest elements (particles). However, either perspective, by itself, is an incomplete representation of reality (since the strengths of the other perspective are unavailable). Therefore, neither approach by itself can serve as a guide to achieve a more complete understanding of ecosystem structure and function.

CEL HYBRID models can provide a more complete perspective for understanding ecosystems than either Eulerian or Lagrangian perspectives by themselves. CEL HYBRID models couple the only two spatial and temporal

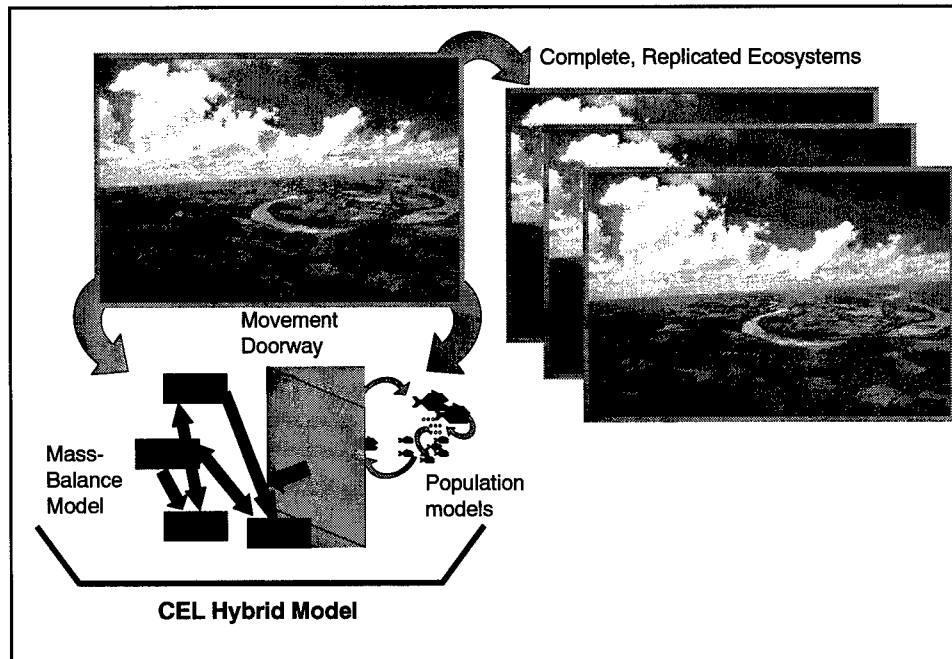


Figure 16. Relationship to CEL HYBRID models and conceptual steps in modeling ecosystems

reference frames for understanding natural processes. There are no other perspectives to be considered. Therefore, the coupled approach has the potential for a total description of complicated processes that neither approach alone can achieve (Tran et al. 1998). By simulating the movement of large or abundant biota, particle tracking logic can be used as a gateway to move back and forth between the two modeling reference frames, as needed, to simulate important processes or components of ecosystems. By coupling Eulerian and Lagrangian reference frames into a single framework, ecosystem scientists have the potential for getting closer to a first principles understanding of natural systems since the coupled reference frames can build on the unique strengths of each perspective.

Considerations of Scale

Levins (1992) identifies determination of scale and pattern as the central problem facing ecologists in their studies of ecosystems. Presently, CEL HYBRID models offer some advantages over either mass-balance or population models separately, because CEL HYBRID models are bi-scalar; that is, they perform simulations at the scale of the Eulerian model and at the scale of the Lagrangian model. The scales at which each of the two submodels in a CEL HYBRID model run do not have to be the same. Therefore, CEL HYBRID models tend to be bi-scalar with the Eulerian model running at a relatively fine temporal and spatial scale and the Lagrangian model (or at least the population dynamic submodel) running at longer temporal and larger spatial scales.

CEL HYBRID models, even though they may have more complete scale representation than their component submodels, still must generally operate over a limited range of scales because of limitations in computational resources. Therefore, application of CEL HYBRID models will require some judgement on the part of the modeler to optimally scale a simulation to address a particular issue. For example, if the focal taxon for a simulation is elephant dung beetles, then the ecosystem must be simulated on a temporal and spatial scale appropriated for dung beetles. Dung beetles are short-lived compared to elephants and respond to their environments at a considerably smaller scale than elephants. In such a case, dung beetles would be simulated by the Lagrangian submodel and elephants and the production of dung beetle food may be best represented in the Eulerian submodel of the CEL HYBRID model. Conversely, if the focal taxon is elephants, then the population dynamics of dung beetles may be best represented by an Eulerian module and the population dynamics of elephants best represented by a Lagrangian framework. Parallel processing may be necessary to include more than a limited number of species populations in a CEL HYBRID model because the description of movement in CEL HYBRID model may be computationally demanding.

Extrapolation to Terrestrial Applications

Although CEL HYBRID models are described for application to aquatic systems, the same basic methods described in this report can be applied to terrestrial or wetland settings in which the spatial information is provided by spatial data as used in Geographical Information Systems (GIS) applications. The interpolation technique used to estimate values for points interior to the nodes or cell faces can be used equally well for nonhydraulic or nonwater quality values. The interpolated values can then be used as the basis of rules to portray movement behavior of terrestrial organisms.

Summary

The following steps are necessary to implement a CEL-HYBRID model (Figure 17): (1) obtain suitable field data for quantitatively describing the behavior of target aquatic biota to selected components of the hydraulic and/or water quality fields; (2) develop and verify a particle tracking algorithm to simulate passive particle transport (the basis for swim path selection in a water quality and/or hydraulic field); (3) develop and verify a statistical model to describe behavioral stimuli responses to water quality and/or hydraulic information; (4) develop the Numerical Fish Surrogate (NFS) that can emulate fish behavior in a simulated environment; (5) simulate the hydraulic and/or water quality field; (6) generate biota response data for decision support; and (7) summarize the data for decision support. These steps are described in detail in the following text.

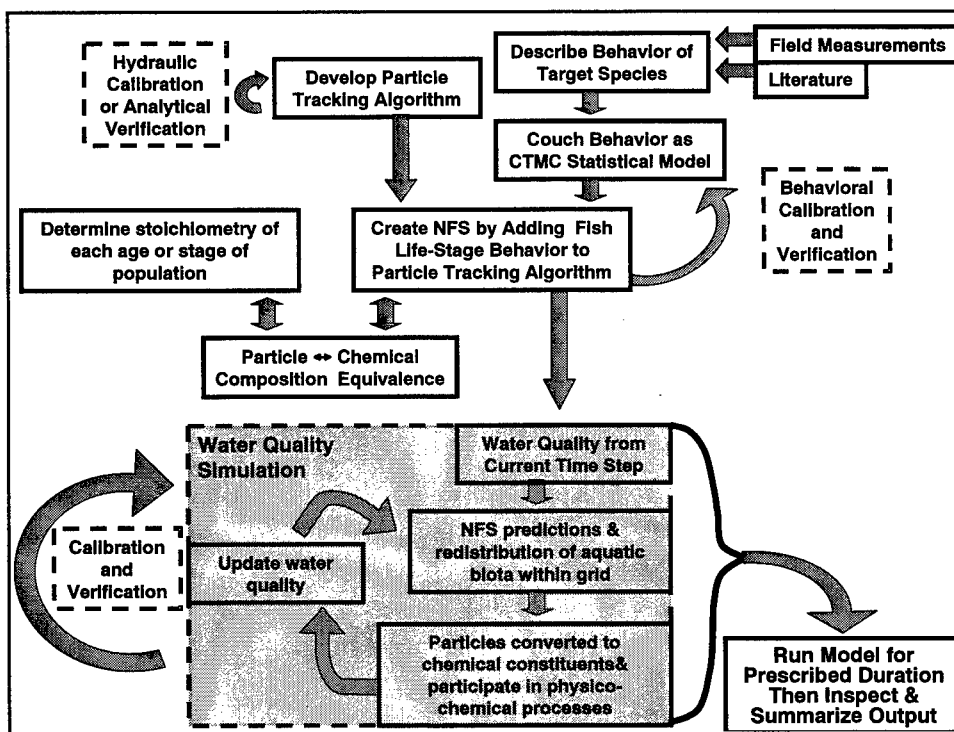


Figure 17. Flowchart of the integrated steps required to use a CEL-HYBRID model. NFS=Numerical Fish Surrogate. CTMC=Continuous-Time Markov-Chain

Step 1 – Obtain suitable field data for quantitatively describing the behavior of target aquatic biota to selected components of the hydraulic and/or water quality fields

Patents are pending on methods to formulate the behavior of target aquatic organisms in hydraulic fields and water quality fields. Relatively high-resolution behavioral data (equal in resolution to available hydraulic and/or water quality data) are required to implement the invention. Either new or existing data can be employed. The behavioral data needed consist of time series of target fish locations collected concurrently with information describing the hydraulic and/or water quality fields where the fish are located. Alternatively, hydraulic and/or water quality information could be obtained from predictions made by numerical or physical hydraulic/water quality models. The simulated hydraulic and/or water quality fields can serve as a template on which behavioral data are superimposed. This facilitates the evaluation of target species' responses to stimuli. Typically, behavioral data consist of traces of fish position as collected by split-beam hydroacoustics (i.e., a sampling method in which a specialized SONAR system is employed to locate fish in 3-D at time intervals of seconds to minutes) or data obtained from radio or acoustic-tagging studies (i.e., some

members of the target species are tagged with radio or acoustic tags and their position in 3-D is determined in time). However, any other gear types that provide spatial and/or temporal fish distributional information in known hydraulic and/or water quality fields can also be employed.

Step 2 – Develop and verify a particle tracking algorithm to simulate passive particle transport (the basis for swim path selection in a water quality and/or hydraulic field)

The particle tracking algorithm emulates the path made by a neutrally buoyant particle that is passively transported. The algorithm is modified to provide the means for simulating the swim path selection of fish or other aquatic organisms. Velocity vectors u (X-direction), v (Y-direction), and w (Z-direction) are obtained from the hydraulic model at nodes and interpolated to interior points of interest. The interpolated velocities are then used to calculate the anticipated position of the simulated fish for the current time-step assuming passive transport. Passive transport (in a faster flowing environment) or random displacement (in a slower flowing environment such as a lake or reservoir) is used to determine the anticipated location of the simulated fish. Water quality and/or hydraulic information at all anticipated locations is assimilated and used to invoke the “stimuli-response rules.” However, beforehand, the accuracy of the particle tracking algorithm must be verified by analytically solving for the streamlines or by tracking a drogue through a real system that is also simulated with the hydraulic model.

Step 3 – Develop and verify a statistical model to describe behavioral stimuli responses to water quality and/or hydraulic information

The behavior of target aquatic species is couched in a CTMC statistical model using data from Step 1.

Step 4 – Develop the Numerical Fish Surrogate (NFS) that can emulate fish behavior in a simulated environment

Integrating the products of Steps 2 and 3 results in a Numerical Fish Surrogate. The NFS estimates how a fish moves in response to hydraulic and/or water quality stimuli in a manner consistent with the natural response of the target biota to similar stimuli. A set of “stimuli-response rules” is used to predict the new location of the target organism. These rules, based on actual fish behavior, transform the passive particle to a virtual fish, thereby, creating a Numerical Fish Surrogate. In Figure 7, a virtual fish moves as a passive particle in the X- and Y-directions, yet moves with increasing dissolved oxygen, opposite of passive transport, in the vertical (Z) direction.

Step 5 – Simulate the hydraulic and/or water quality field

Unique hydraulic and/or water quality conditions are associated with every design, siting, size, and operational scenario. The hydraulic and water quality fields can be simulated using 1-, 2-, or 3-D (preferred) hydraulic/water quality models. Alternatively, measurements of the flow and water quality fields can be obtained at the site.

Step 6 – Generate biota response data for decision support

Physical, chemical, and biological predictions of the ecosystem model are output.

Step 7 – Summarize the data for decision support

Data is summarized for analysis, assessment, and decision-making.

Conclusions

Management and modification of water resources (e.g., construction of instream structures, regulatory actions, operating strategies, etc.) have a profound effect on the physico-chemical environment of aquatic ecosystems and on the living resources that depend on this environment. CEL HYBRID models offer a way to couple Eulerian and Lagrangian reference frames so higher trophic levels of an aquatic ecosystem, such as fish and shellfish, can be systematically and realistically simulated. CEL HYBRID models have the potential to partially address the problem identified by Alewell and Manderscheid (1998) that some biological processes are inherently too difficult to simulate. CEL HYBRID models allow for the analysis of higher trophic level processes with minimal distortion and loss of information by coupling the two frames of reference and exploiting the advantages and minimizing the disadvantages associated with each.

Patents are pending on methods used to simulate movement that can be used to implement CEL HYBRID models and also on the use of CEL HYBRID models as an improved method for simulating population dynamics in an ecosystem context.

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